Influence of Hydrologic Processes on Reproduction of the Introduced Bivalve *Potamocorbula amurensis* in Northern San Francisco Bay, California[1]

Francis Parchaso and Janet K. Thompson[2]

Abstract: Monthly censusing of reproductive condition of the Asian clam *Potamocorbula amurensis* at four sites in northern San Francisco Bay over a 9-yr period revealed year-to-year differences in local reproductive activity that are associated with patterns of hydrologic variability. Between 1989 and 1992, Northern California experienced a drought, whereas the period between 1993 and 1998 was marked by a mix of wet and dry years. We took advantage of the extreme year-to-year differences to examine reproductive responses to river inflow patterns. Populations of *P. amurensis* at the upstream sites in Suisun Bay and Carquinez Strait were more reproductively active during wet years than dry years. Conversely, at the downstream site in San Pablo Bay, the population was more reproductively active during dry years than wet years. We suggest that the different reproductive patterns observed reflect the clam's response to different sources of food. During wet years, organic matter from the rivers augments food supplies in Suisun Bay. During dry years, when inflow into the San Francisco Bay Estuary from the rivers is reduced, water transported from the adjacent ocean into the estuary as far as San Pablo Bay provides a supplemental food supply for the local production. The populations take advantage of these spatially distinct food supplies by initiating and maintaining local reproductive activity. We conclude that the ability of *P. amurensis* to consume and use various types of food to regulate its reproductive activity is part of the reason for its success as an invasive species.

THE ASIAN CLAM *Potamocorbula amurensis*, a native of East Asia, Khabarovsk (a republic of the former Soviet Union), and Korea, was introduced into San Francisco Bay in 1986. The success with which *P. amurensis* colonized and established itself in the benthic community of San Francisco Bay has been well documented (Thompson et al. 1988, Carlton et al. 1990, Nichols et al. 1990), although the reasons for its success have not been discussed. In this period of accelerating rates of exotic species introductions in estuaries, and in San Francisco Bay in particular (Cohen and Carlton 1998), the mechanisms of the successful spread of a species following inoculation is of growing interest. In a 2-yr period (1986–1987) *P. amurensis* spread throughout San Francisco Bay, occupying a variety of intertidal and subtidal substrates (sand, clay, mud, peat, and combinations thereof) in a wide range of salinities (1 to >30 psu) (Carlton et al. 1990). The spatial success of *P. amurensis* is acutely relevant in this estuary because *P. amurensis* is an efficient filter feeder, able to filter food ranging in size from bacteria to copepod larvae (Werner and Hollibaugh 1993, Kimmerer et al. 1994). Several authors (Cloern 1982, Nichols 1985) have suggested mechanisms by which the filter-feeding benthos, primarily bivalves, can control phytoplankton biomass in both South and North San Francisco Bay, and Alpine and Cloern (1992) hypothesized that *P. amurensis*

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[2] U.S. Geological Survey, Water Resources Division, Menlo Park, California 94025.

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is responsible for the disappearance of the annual phytoplankton bloom in the northern bay. The continuing dominance of *P. amurensis* in San Francisco Bay has also resulted in changes in the San Francisco Bay ecosystem by altering both benthic community structure and interspecific dynamics (Nichols et al. 1990).

An important component in the spatially extensive success of *P. amurensis* is its ability to reproduce and recruit into established benthic communities under highly variable conditions characteristic of the estuarine environment. In this study, we examined connections between patterns of change in the estuary's hydrologic regime and the reproductive patterns of *P. amurensis* during a 9-yr period at four sites along the salinity gradient in northern San Francisco Bay. We show that *P. amurensis* successfully reproduces in northern San Francisco Bay every year, and that local reproductive patterns within each year are related to spatial and temporal changes in the hydrologic conditions and thus in the food supply along the salinity gradient of the estuary. The success of *P. amurensis* in this system is therefore related to its ability to use a variety of food sources and the apparent lack of temperature or salinity control on reproductive activity.

Hydrologic Setting

The drainage basin of the Sacramento–San Joaquin River system (Figure 1) is the source of 90% of the freshwater inflow into San Francisco Bay (Conomos et al. 1985). Freshwater flow within this river-estuary system, although managed by dams and diversions, is seasonal, composed of rainfall runoff in the winter and snowmelt in the spring and early summer. The adjacent Pacific Ocean is the

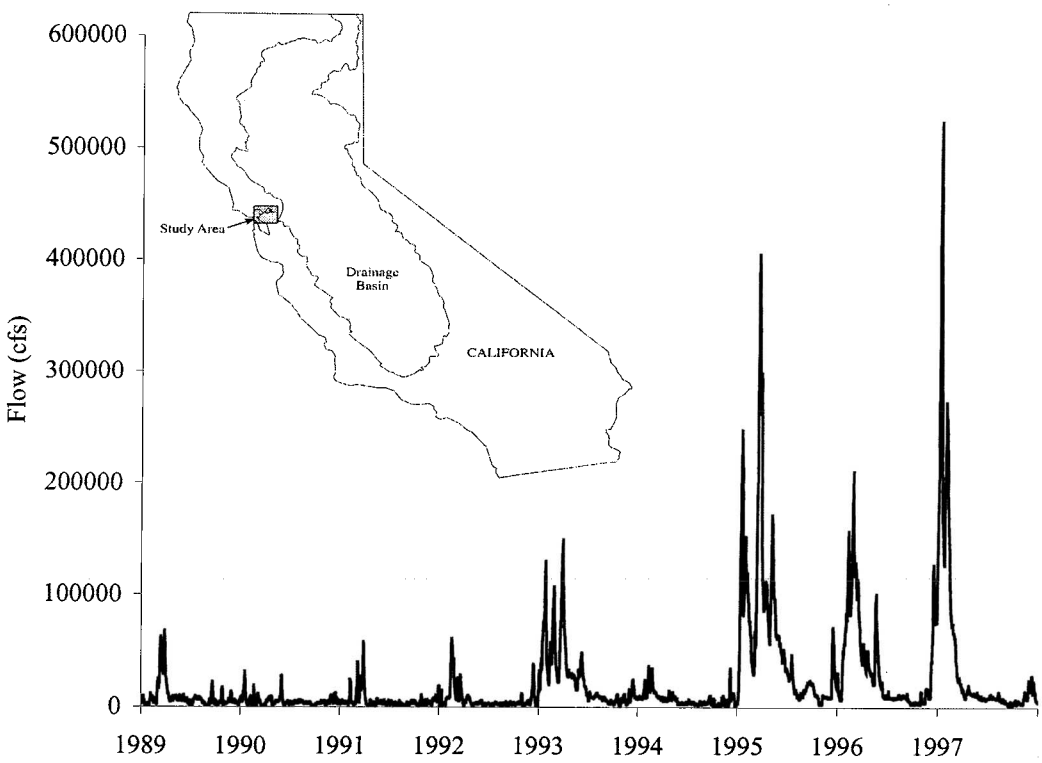


FIGURE 1. Freshwater flow from the drainage basin of the Sacramento and San Joaquin Rivers into San Francisco Bay. Inset shows study area.

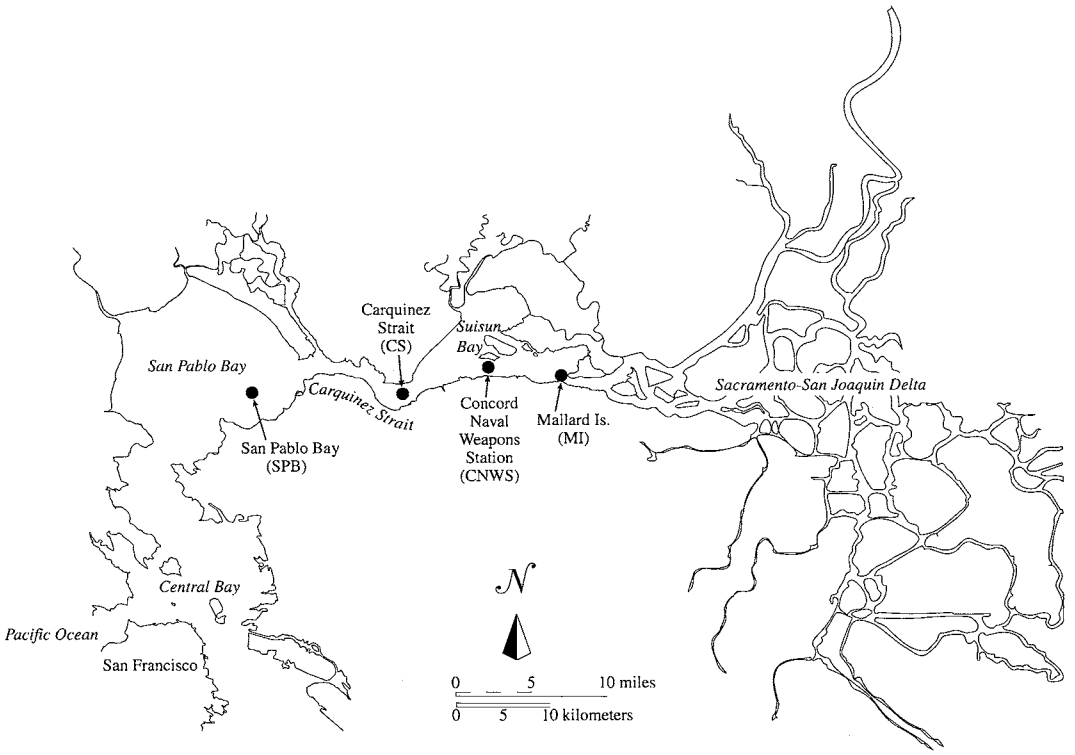


FIGURE 2. Northern San Francisco Bay and Sacramento and San Joaquin River Delta showing collection sites in central San Pablo Bay, Carquinez Strait, and Suisun Bay. All stations are located in the deep-water shipping channel.

source of saline water that is transported tidally into San Francisco Bay through the Golden Gate (Figure 2). The extent of the marine influence on the salinity gradient within San Francisco Bay is highly seasonal. In dry summers, saline water can reach as far as the confluence of the Sacramento and San Joaquin Rivers. During extremely wet winters low-salinity water (<10 psu) can be found throughout northern San Francisco Bay and beyond the Golden Gate (Conomos et al. 1985).

During this study, California experienced a 6-yr drought that ended in 1993 (Figure 1). The following year, 1994, was also a dry year. The California Department of Water Resources classified the remaining years of this study (1995–1997) as wet years. The differing hydrologic conditions during this study provide a contrast in environmental influences that coincide with changes in the reproductive behavior of *P. amurensis.*

Bivalve Reproductive Strategies

Giese and Pearse (1974, 1979), in their review of reproduction in bivalves, described many exogenous regulators of gametogenesis. As an example, they pointed out that it is important that marine invertebrates reproduce at a time when the young have a good chance of surviving (e.g., when temperatures, salinity, or food conditions are favorable for larval survival). Often, reproductive activities such as gametogenesis are begun much in advance of such favorable conditions, indicating that some environmental changes must act as early cues to synchronize reproduction with the subsequent favorable conditions. These environmental changes represent an indirect

exogenous control on reproduction. Such environmental changes need not be restricted to a single factor, but may consist of several factors that, when operating together, can externally stimulate synchrony of reproductive activities.

Studies of the reproductive cycles of other introduced bivalves common in San Francisco Bay show that bay populations tend to have longer reproductive seasons than are reported for conspecific populations on the Atlantic and Pacific Northwest coast of North America. For example, Rosenblum and Niesen (1985) found that *Mya arenaria* was reproductively active from March through November in San Francisco Bay, a reproductive season 2 months longer than seen in populations in the state of Washington. Pacific coast populations of *M. arenaria* also have a single reproductive season, whereas Atlantic coast populations have a biannual reproductive cycle. These differences in the reproductive cycle of *M. arenaria* have been attributed to differences in temperature regimes: San Francisco Bay has a longer period of optimum temperatures than in Washington; favorably warm temperatures occur initially between March and April and secondarily between June and July on the East Coast (Rosenblum and Niesen 1985).

Varon (1978) found a similarly long reproductive season in *Venerupis japonica*, a native of Japan, in San Francisco Bay (April through October), which is slightly longer than that of the same species in Washington (April through September). He also noted that populations in Japan have biannual spawns and suggested that the differing temperature regimes among the three locations may be responsible for their different reproductive patterns.

Previous studies of reproduction in *P. amurensis* and congeneric species have described the reproductive behavior and suggested environmental factors that may influence reproduction. In San Francisco Bay, Parchaso (1995) found that *P. amurensis* is dioecious, begins reproducing at approximately 4 mm in length, and has both seasonal reproduction in Suisun Bay and near-continuous reproduction in South San Francisco Bay. Furthermore, temperature and salinity changes were not controlling factors of reproduction. That earlier work was conducted during the previously mentioned 6-yr drought.

Carlton et al. (1990) reviewed reproduction literature for a congeneric species in Asia, *Potamocorbula laevis*, and found that this species undergoes gametogenesis between mid-September and mid-October when water temperature is between 12 and 23°C. *Potamocorbula laevis* is primarily dioecious, with a few hermaphrodites observed. Fertile eggs are released when water temperature is between 16 and 20°C. Metamorphosis to a veliger larva occurs after 20 to 22 days, and settlement occurs after 30 to 40 days at a size of 370 μm.

Study Locations

Northern San Francisco Bay is a partially mixed estuary dominated by seasonally varying river flow from the Sacramento and San Joaquin Rivers, which are fed by numerous tributary rivers and streams that drain the Sierra Nevada Range (Figure 1). Our four sampling sites are located in three different regions along the salinity gradient of the northern San Francisco Bay estuary: (1) Suisun Bay, (2) Carquinez Strait, connecting San Pablo Bay and Suisun Bay, and (3) San Pablo Bay (Figure 2). These regions were selected to represent different environmental characteristics, each with distinct patterns of variation in physical characteristics (e.g., temperature and salinity) at the sites.

The Mallard Island station (MI) is located near the confluence of the Sacramento and San Joaquin Rivers (Figure 2). During the winter and spring, salinities can be as low as 0 psu and temperatures can be as low as 4°C. During the summer and fall, salinities range from 10 to 15 psu and temperatures can reach 23°C (Conomos 1979, Cloern and Nichols 1985).

The Concord Naval Weapons Station (CNWS) site is located north of the Concord Naval Weapons Station in the southern part of Suisun Bay and in the deep-water shipping channel (Figure 2). The salinity and temperature characteristics are similar to those at MI.

The Carquinez Strait station (CS), located in the narrow channel that connects Suisun and San Pablo Bays (Figure 2), is characterized by high tidal current velocities and enhanced vertical tidal mixing (Walters et al. 1985). Carquinez Strait is a transitional zone between San Pablo Bay and Suisun Bay, with salinities ranging from 2 psu in the winter to 15 psu in the summer (Conomos et al. 1985) and temperatures ranging between 10 and 20°C (Conomos 1979).

The San Pablo Bay site (SPB), in the large embayment west of Carquinez Strait, is located on the edge of the shipping channel east of Pt. Pinole (Figure 2). San Pablo Bay salinities range from 20–28 psu in the spring to 24–30 psu in the fall, and temperatures range from 8°C in the winter to 18°C in the summer (Conomos et al. 1985). Seasonal freshwater and marine influences characterize the SPB site.

MATERIALS AND METHODS

Potamocorbula amurensis specimens were collected monthly from the four subtidal stations, from October 1989 to December 1997, to determine their reproductive condition. Clams were collected with a Van Veen grab (0.05 m^2) and preserved in 10% buffered formalin. In the laboratory, 10 to 15 clams representing the full size range available at each station were examined for each sampling date. Minimum sample size was 10 except during months when tissue samples were damaged during the histological processing or when animals were difficult to collect.

The visceral mass of each clam was removed and stored in 70% ETOH. The tissues were prepared using standard histological techniques. The embedded samples were thin sectioned using a microtome and then stained with Harris' hematoxylin and eosin. The stained thin sections were examined with a light microscope. Each specimen was characterized by sex and developmental stage of the gonads, thus allowing each specimen to be placed in one of five qualitative stages of gonadal development: inactive, active, ripe, spawning, and spent.

Individuals at each reproductive stage at each station were tabulated and the data converted to percentages. Although five gonadal stages were defined, gonadal development in many of the clams was continuous, and the clams were commonly in transition between stages (e.g., developing from active to ripe). To alleviate the difficulty in determining the developmental stages of clams in transition between the defined stages, the percentages of clams in the active, ripe, and partially spent stages were given positive values (multiplied by +1), and the percentages of clams in the inactive and spent stages were given negative values (multiplied by −1). These values were summed for each month at each station, and these represent the "central tendency of reproduction." For example: a month with 30% active, 10% ripe, and 70% inactive clams would be scored as −30%. A Kruskal-Wallis one-way analysis of variance (ANOVA) was used to test significance among the monthly central tendencies. The coefficient of variation of each month was used to compare the variation in reproduction between wet and dry years.

To characterize the physical and biological environment of northern San Francisco Bay during our study, we used temperature, salinity, and chlorophyll data collected by other agencies. The California Department of Water Resources (CDWR) collected Mallard Island and Carquinez Strait salinity and temperature data every hour using an in situ surface conductivity and temperature sensor (California Department of Water Resources 1999). San Pablo Bay data were collected every 15 min by the U.S. Geological Survey (USGS) using in situ conductivity and temperature sensors on the surface and bottom (Buchanan 1999). These salinity and temperature data were summarized to acquire a mean monthly value for wet and dry years. Chlorophyll *a* flux was calculated as described by Jassby et al. (1993): multiplication of the characteristic surface chlorophyll *a* concentration of the Sacramento and San Joaquin Rivers by their outflow rates. These values represent the estimated carbon from microalgae that are transported into the bay from the freshwater tributaries. Because primary production can be high in these areas, the carbon flux can be substantial (Jassby et al. 1993). Chlorophyll *a* concentrations for the

chlorophyll flux calculation and for chlorophyll *a* concentrations at the MI, CNWS, CS, and SPB sites and for central San Francisco Bay were provided by the USGS (Wienke et al. 1990, 1991, 1992, 1993, Caffrey et al. 1994, Edmunds et al. 1995, 1997, Baylosis et al. 1997, 1998). Kendall's Tao and Kendall's concordance correlations were used to test significance between reproductive central tendency and physical parameters.

RESULTS

Reproductive Patterns

Potamocorbula amurensis reached reproductive maturity (i.e., sperm and eggs were present) each year at all four locations. Reproductively active individuals were observed in salinities as low as 0.1 psu (spring, Suisun Bay) and as high as 27.6 psu (summer, San Pablo Bay) and at temperatures ranging from 6.4°C (winter, Suisun Bay) to 23.0°C (summer, Suisun Bay). There were marked temporal differences in the central tendency of reproduction among the populations of *P. amurensis*.

WET YEARS. During wet years (1993, 1995, 1996, and 1997), a greater percentage of individuals at the stations closer to freshwater inflow (MI and CNWS) were reproductively active than individuals during dry years (Figure 3). The reproductive central tendency of the MI population (the closest to freshwater inflow) showed reproductive activity for 10 months during wet years. The only months of reproductive inactivity were June and October. The population at the next closest down-bay station, CNWS, was active for 9 months. The populations at the stations closer to the marine influence, CS and SPB (Figure 3), were active for shorter periods (8 months) than the populations at the fresher locations.

DRY YEARS. Reproductive activity was shorter in duration and a smaller percentage of individuals were reproductive during the dry years (1989–1992, 1994), relative to the wet years, at the stations closest to freshwater inflow (MI, CNWS, and CS) (Figure 3). Although there was reproductive activity from January through May at MI, the percentages of reproductive individuals during dry years show a consistent trend of being lower than the percentages during wet years. During the summer and fall, reproductive activity was observed only in September. The MI population initiated reproductive activity again in November and December. Reproductive activity in the CNWS population was of a lesser magnitude and shorter duration during dry years than during wet years. The CNWS and CS populations were active for 4–5 months, primarily from January through April and then again in December at CNWS. SPB animals showed an opposite trend from that seen at the other sites, with reproductive activity greater in duration and in magnitude for most months during the dry years than during wet years (Figure 3). The SPB population was reproductively active from January to May and again from July through December.

The coefficients of variation for the central tendencies were in phase for dry and wet years during the winter and spring for populations at the freshest station, during winter and fall at MI and CNWS, although the coefficient of variation was larger, with one exception, in the dry years at these stations (Figure 4). Peaks in the monthly coefficient of variation at CS were out of phase for the wet and dry years only during spring. The coefficients of variation for the CS population (Figure 4) peaked in summer and fall during the wet years and dry years. Conversely, the coefficient of variation for the CS population was very high in spring of dry years, but the wet-year coefficient of variation was at an annual low during spring. The variability of SPB central tendency values in wet and dry years was mostly out of phase with the greatest variability occurring during the late spring in the dry years and the late summer in the wet years.

DISCUSSION

Interannual differences in freshwater inflows from the Sacramento and San Joaquin Rivers are shown by marked differences in salinity distributions in the estuary. Although the daily average salinity dropped between January and April during every year of the study,

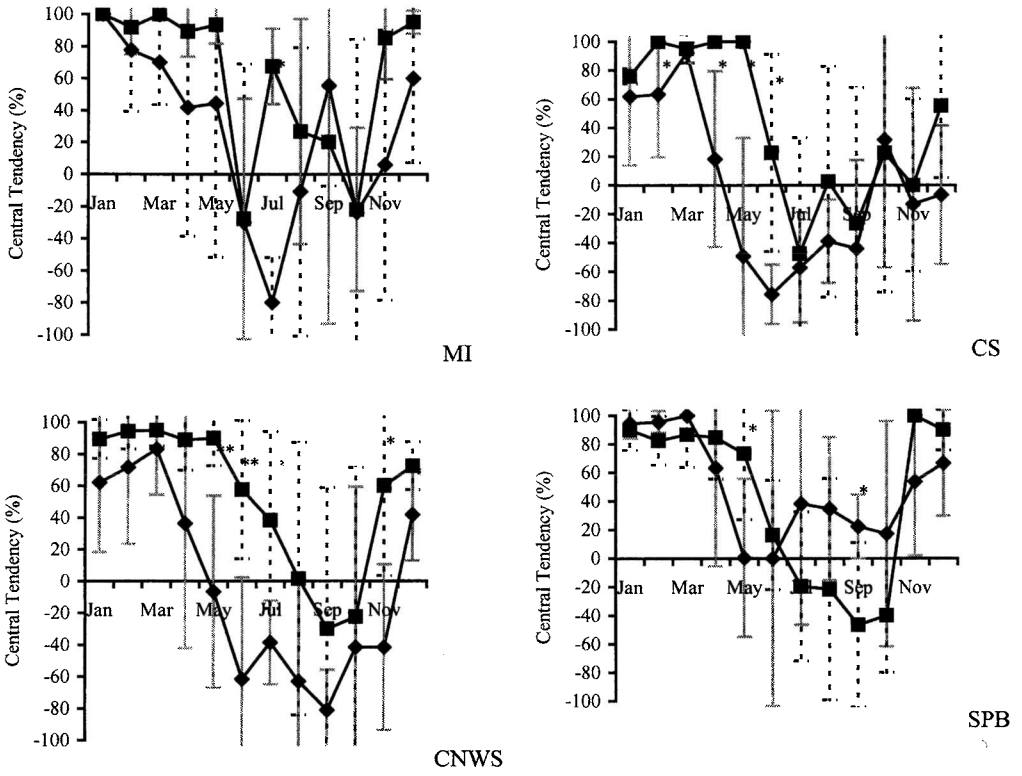


FIGURE 3. Mean monthly central tendency (percentage with 1 SD) of reproductive (positive) and nonreproductive (negative) populations at the Mallard Island (MI), Concord Naval Weapons Station (CNWS), Carquinez Strait (CS), and San Pablo Bay (SPB) locations during pooled wet (■) and dry (◆) years. Central tendency (y axis) is an index that combines the percentage of reproductive individuals (active, ripe, and spawning, see text for definitions) and nonreproductive individuals (inactive and spent). For clarity nonreproductive central tendency values are given negative values. Periods of significant differences between wet and dry years are indicated (*, $P < 0.10$; **, $P < 0.05$).

corresponding to periods of freshwater inflows, dry years obviously had substantially higher average salinities than wet years. The salinity at the most up-stream station, Mallard Island, and the down-stream station, Carquinez Strait, dropped to 0 psu in the wet years (Figure 5).

Spatial differences in salinity reflect the estuarine nature of northern San Francisco Bay. Mallard Island, the location farthest upstream, had the lowest mean monthly salinity values and narrowest range (0 to 10 psu) (Figure 5). In contrast, the mean monthly salinity in San Pablo Bay showed a strong marine influence and ranged from 12 to 29 psu. The variability in the mean monthly salinity at the Carquinez Strait station was the greatest of all the stations sampled, ranging from 2 to 22 psu (Figure 5).

Reproductive individuals of *P. amurensis* were found throughout the salinity range investigated in this study. However, reproductive seasonality was not consistent among the stations. For example, the Suisun Bay populations (MI and CNWS) of *P. amurensis* demonstrated a seasonal reproductive cycle that was characterized by a high percentage of reproductive individuals during wet years. In contrast, the San Pablo Bay population, the most marine station, had near-continuous reproductive activity during the high-salinity dry years.

Fluctuations in salinity, particularly in shallow marine areas and estuaries that expe-

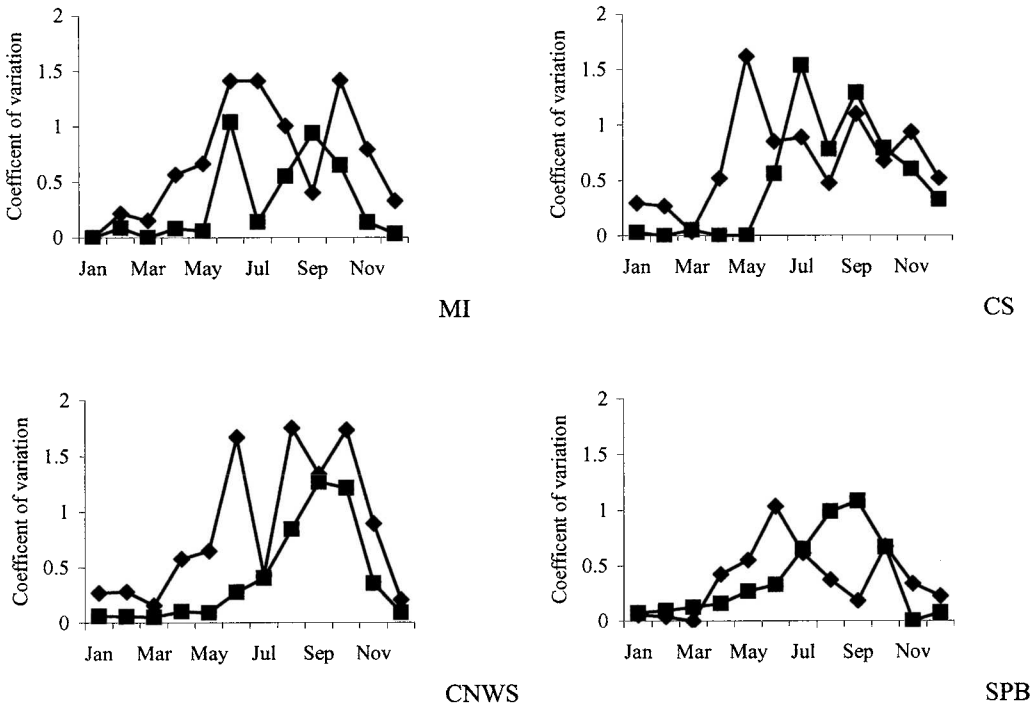
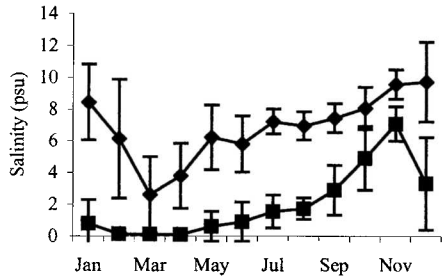


FIGURE 4. Variability of central tendency of individuals at the Mallard Island (MI), Concord Naval Weapons Station (CNWS), Carquinez Strait (CS), and San Pablo Bay (SPB) locations during pooled wet (■) and dry (◆) years.

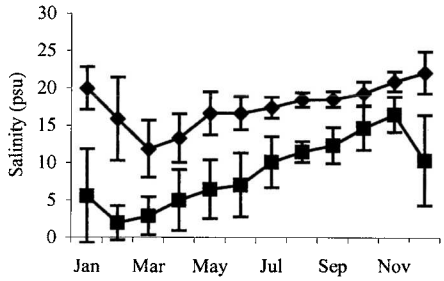
rience large and prolonged changes in salinity during periods of heavy rainfall, have been suggested as possible factors for regulating reproduction in some marine invertebrates (Giese and Pearse 1974, 1979). For example, Wilson (1969) showed that gametogenesis and spawning in a Western Australian estuarine mussel, *Xenostrobus securus*, are related to salinity fluctuations, and that spawning occurs at different times in several populations, in each case correlated with a critical salinity level. The onset of gametogenesis, maturation of gametes, and spawning occurs in synchrony with periods of rainfall each year, regardless of the timing of the rainfall periods and thus regardless of temperature within a given year. We show here that the processes that determine patterns of salinity (i.e., freshwater flow) also appear to control the reproductive patterns of *P. amurensis* in northern San Francisco Bay, but that neither salinity nor temperature are, by themselves, controlling factors of reproduction.

The recorded average mean monthly temperature at all locations showed seasonal variability (Figure 5) and little interannual variation. There was little spatial variability in the mean monthly values. Throughout the sample locations, the mean monthly temperatures ranged from 8 to 22°C. Reproductive activity at all the stations was observed throughout the observed temperature range (Figure 6).

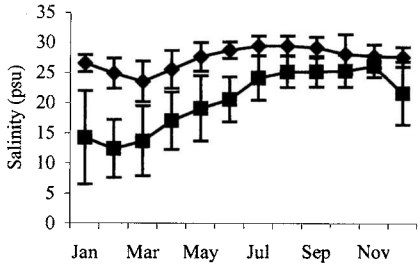
The differences in reproductive patterns between wet and dry years in Suisun Bay are associated with variations in freshwater flow into Suisun Bay from the Sacramento and San Joaquin Rivers, but are not specifically related to some critical salinity, temperature, or volume of freshwater flow. We suggest that the seasonality of reproduction in Suisun Bay populations is linked to the seasonal nature of locally produced phytoplankton and river-borne food supplies. Because of its ability to efficiently filter and assimilate a wide range of particle sizes and food types, from



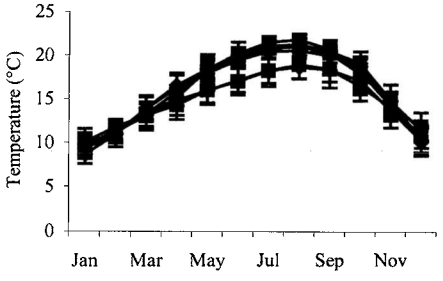
Salinity MI



Salinity CS



Salinity SPB



Temperature for all stations

FIGURE 5. Mean monthly salinity (psu) at the Mallard Island (MI), Carquinez Strait (CS), and San Pablo Bay (SPB) locations during pooled wet (■) and dry (◆) years; mean monthly temperature (°C ± 1 SD) at the Mallard Island, Carquinez Strait, and San Pablo Bay locations during pooled wet (■) and dry (◆) years.

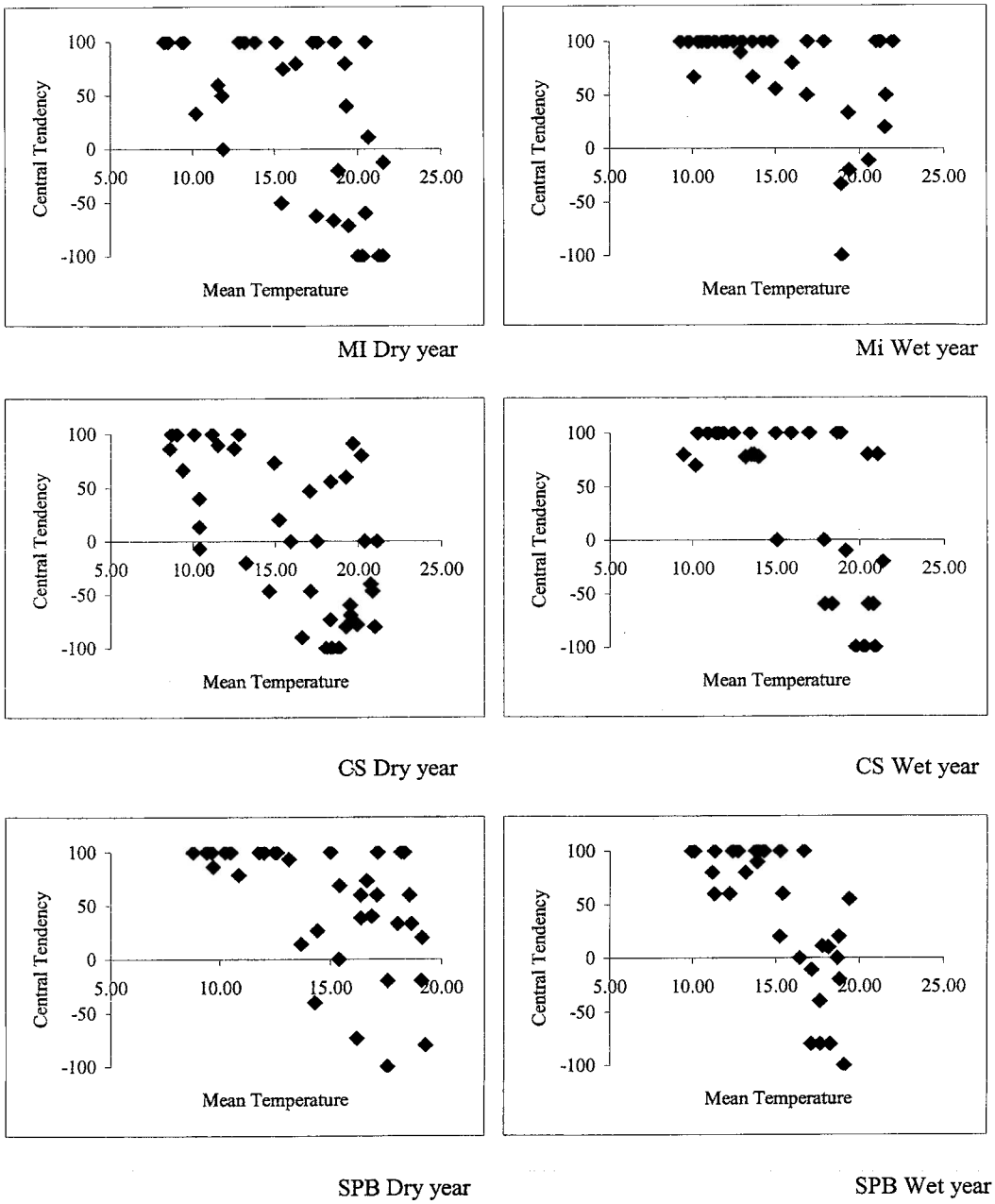


FIGURE 6. Scatter plot of temperature versus central tendency (see text) at the Mallard Island (MI), Carquinez Strait (CS), and San Pablo Bay (SPB) locations during pooled wet and dry years.

phytoplankton to free and particle-bound bacteria (Decho and Luoma 1991, Werner and Hollibaugh 1993), *P. amurensis* is able to use a variety of food resources. We know that the seasonal patterns of freshwater flow are directly related to the quantity and quality of carbon in this system. Up to 75% of the carbon found in Suisun Bay could be traced to

riverine inputs (Jassby et al. 1993) before the elimination of the phytoplankton bloom in 1987. With the introduction of *P. amurensis* to the system, allochthonous sources of carbon are likely to be even more important than autochthonous sources of carbon (Schemel et al. 1996). We also know that the timing of freshwater inputs is critical to the quality of food available to organisms in Suisun Bay. Although freshwater transports suspended solids from the Sacramento and San Joaquin Rivers into Suisun Bay, the relationship between freshwater outflow and suspended solid concentration and the concentration of labile carbon is not correlated. The initial pulse of freshwater from the first rains of the rainy season, usually in the late fall or early winter, is the greatest source of suspended solids into Suisun Bay (Ruhl and Shoelhammer 1997) and is likely to be a combination of near-field watershed and marsh sediments and particulate matter (Jassby and Cloern 2000). Subsequent rain and snowmelt events transport suspended solids downstream but not at the same magnitude or with the same high percentage of labile carbon (Canuel and Cloern 1996) as the first pulse of the rainy season.

Food transported into Suisun by way of this first freshwater pulse may be the energy source that initiates reproductive activity in *P. amurensis* in winter. This is the most consistent reproductive cue seen for *P. amurensis* during all wet years as shown by the low variability in positive reproductive activity during this period (i.e., the coefficient of variation of the reproductive central tendency was consistently low during wet winters) (Figure 4). The lack of large storms during dry years produces less particulate carbon (Jassby and Cloern 2000) and is less likely to produce a large, one-time pulse of particulate carbon from the spatially disparate sources of carbon, the distant watershed and nearby marshes. As we might expect, this cue was less temporally consistent during the dry years and the coefficients of variation during winter were thus larger in dry years than in wet years. Because this cue for initiation of reproduction is not linearly related to freshwater flow (i.e., maximum reproductive activity does not occur at minimum or maximum freshwater flow volumes), we would not expect, nor do we see, a strong correlation between these variables (Table 1).

It is likely that some riverine sources of food are supplied to *P. amurensis* throughout the year. It is unknown what percentage of the suspended solids that are transported into the bay contain bioavailable carbon at the time of transport and how much is transformed in transit. It is clear that there are bacteria living on these particles once they enter the bay and that they are both productive (Hollibaugh and Wong 1996) and sea-

TABLE 1

Significant Kendall's Tao and Kendall's Concordance Values for Central Tendency Versus Chlorophyll *a* Concentration, Chlorophyll *a* Flux, and Freshwater Flow for Pooled Wet and Dry Years

Station	Water Year	Factor	Kendall Tao	Factor	Kendall Concordance
MI	Dry	—		Chlorophyll *a* and chlorophyll flux	0.87***
	Wet	Freshwater flow	0.30*	Chlorophyll *a* and chlorophyll flux	0.77***
CNWS	Dry	—		Chlorophyll *a* and chlorophyll flux	0.75***
	Wet	Chlorophyll *a*	0.46***	Chlorophyll *a* and chlorophyll flux	0.76***
		Chlorophyll flux	0.41***		
CS	Dry	—		Chlorophyll *a* and chlorophyll flux	0.75**
	Wet	Chlorophyll *a*	0.50***	—	
		Chlorophyll flux	0.28*		
SPB	Dry	—		Chlorophyll *a* and chlorophyll flux	0.87**
	Wet	Chlorophyll flux	0.37***	Chlorophyll *a* and chlorophyll flux	0.80***

Note: Significantly related physical factors were not included in these analyses.
*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

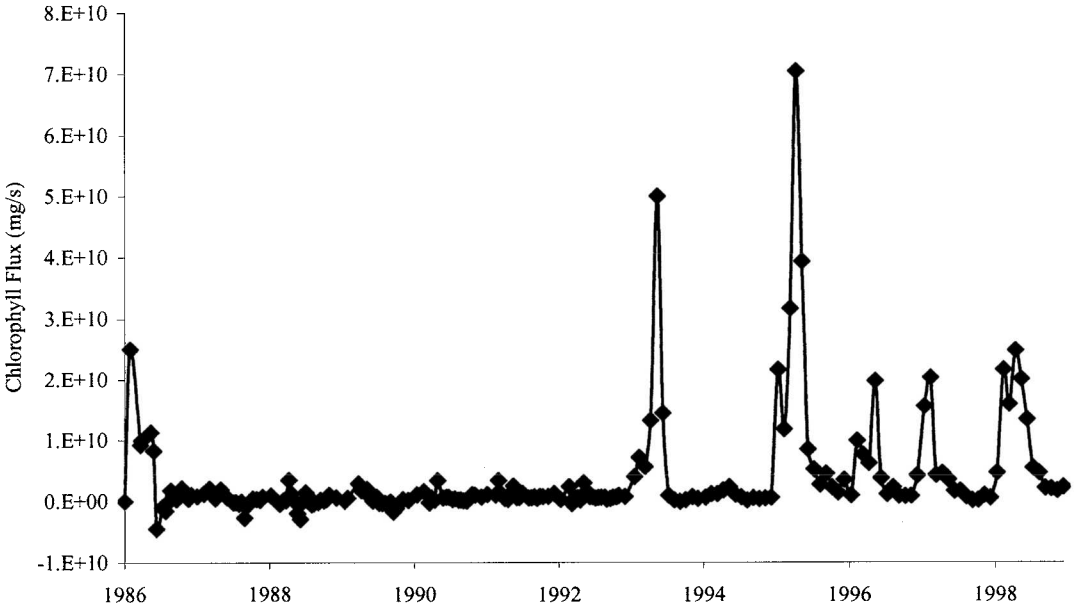


FIGURE 7. Chlorophyll *a* flux into Suisun Bay from the Sacramento–San Joaquin River Delta from 1986 to 1998.

sonally varying (Murrel et al. 1999). The abundance of particle-associated bacteria remains constant between April and July, and declines in August during which time the abundance of free-living bacteria concurrently increases (Murrel et al. 1999). Because *P. amurensis* is capable of feeding on free-living bacteria (Werner and Hollibaugh 1993), it is likely that riverine sources of carbon throughout the year are providing, at the least, a source of bacterial food, if not particulate food. The consumption of this food source by *P. amurensis* may contribute to the summer decline in particle-associated bacteria (Murrel et al. 1999).

Locally produced phytoplankton and phytoplankton transported from other regions in the system are likely to be additional sources of food for *P. amurensis*. Phytoplankton production in the bay and in the rivers is highest in the spring through late summer due to seasonal increases in hydraulic residence times and irradiance. Although phytoplankton biomass has declined in the northern bay since 1987, the higher primary production during these seasons is likely to increase the importance of phytoplankton as a food supply to *P. amurensis* during spring and summer. The positive rank correlation between central tendency and chlorophyll *a* concentration at two of the four sites (Table 1) supports this hypothesis. Phytoplankton from the tributaries also enters the bay as bioavailable carbon when phytoplankton growth rate exceeds respiration and consumption in the Sacramento–San Joaquin Delta. Freshwater phytoplankton is transported into Suisun Bay throughout the year, but a peak in this transported carbon (shown as chlorophyll *a* flux, Figure 7) occurs when peak flows and high chlorophyll *a* concentrations are coincident. The amount of chlorophyll *a* transported into Suisun Bay during wet years was substantially greater than during dry years.

We suggest that food inputs from later freshwater pulses are the cue that determines the length of reproductive activity in spring. During wet years, freshwater input is protracted and food sources such as riverine phytoplankton become available to even the most down-bay populations. The magnitude of chlorophyll *a* flux into Suisun Bay from the delta varied little in magnitude during dry years (1989–1992 and 1994), but consistently

peaked during the spring. Chlorophyll *a* flux during the wet years also peaked during the spring, but at a greater magnitude and for a longer period than in dry years (Figure 7). This higher chlorophyll *a* flux during wet-year springs may be responsible for the protracted reproductive activity during wet years. Reproductive periods were 3 months longer during wet years than during the dry years and were significantly related to chlorophyll *a* flux at the midgradient stations (CNWS and CS). Chlorophyll *a* flux was low during dry years (Figure 7), and this food source may have been depleted and diluted as it was transported down the bay. Consistent with this pattern, clams at the station closest to the freshwater source and closest to the transport of riverine phytoplankton (MI) have a longer reproductive period during dry years than the down-bay populations (Figure 4).

The temporal pattern in the coefficients of variation supports these hypotheses. The low coefficient of variation (i.e., synchronous reproductive activity) during wet springs is due to a strong seasonal cycle in chlorophyll *a* flux. The timing of the chlorophyll *a* flux peak is controlled by a combination of the timing of sufficient river outflow to transport the river-borne phytoplankton into the bay and the seasonal increase in phytoplankton growth rate. The peak chlorophyll *a* flux is thus a function of the seasonally consistent irradiance cycle; spring river outflow is mostly a result of snowmelt that occurs in May and June (Cayan et al. 1997), and phytoplankton growth rate is primarily controlled by light availability in this system (Lehman 1996). Thus, it is not the period of maximum outflow or maximum chlorophyll *a* concentration that controls the peak chlorophyll *a* flux, but the period when their product peaks, which is most related to irradiance. As we might expect, the pattern of freshwater flow during dry springs, with varying amounts of low snow accumulation and varying levels of irradiance needed to melt the snow, is less consistent between years because snowmelt maxima are a function of both snow accumulation and irradiance (Cayan et al. 1997). Thus, interannual variability in the snowmelt runoff during dry years leads to more variability in this food signal and thus in more seasonally variable reproductive activity during the dry years; note that chlorophyll *a* flux was never significantly related to *P. amurensis* reproduction in dry years (Table 1). This increased variability in reproductive activity is true even at the freshest station, which is most likely to benefit from this food source during low runoff years.

It would be helpful to examine the relationship of the combination of these physical factors with central tendency to establish their additive effects. However, the established important physical factors, local chlorophyll *a*, chlorophyll *a* flux, and freshwater inflow, are frequently related to each other (i.e., freshwater flow is commonly related to chlorophyll *a* flux, particularly in dry years, and local chlorophyll *a* concentrations can include chlorophyll *a* that is being delivered from the rivers if the freshwater phytoplankton are still viable). Given these constraints we were able to test the significance of the relationship of local chlorophyll *a* concentration, chlorophyll *a* flux, and central tendency during all but one period (Table 1). In all cases tested, there was a significant relationship (Kendall's concordance ranges from 0.75 to 0.87), and the significance of the combined physical factors was similar to, or greater than, that seen with simple rank correlations.

We hypothesize that the San Pablo Bay populations showed distinctly different reproductive patterns than Suisun Bay populations due to the different sources of food used by these populations. San Pablo Bay populations may receive food from a combination of freshwater, marine (central bay), and locally derived sources. During dry years, phytoplankton biomass and primary production in San Pablo Bay is usually greater than in Suisun Bay (Alpine and Cloern 1992), which was the case in this study for all but 1 yr (Figure 8). In addition, local chlorophyll *a* concentrations are more likely to be augmented by oceanic phytoplankton during the spring and summer due to larger tidal excursions into San Pablo Bay during low runoff periods. Chlorophyll *a* concentrations in central San Francisco Bay (Figure 8), the most marine region of San Francisco Bay,

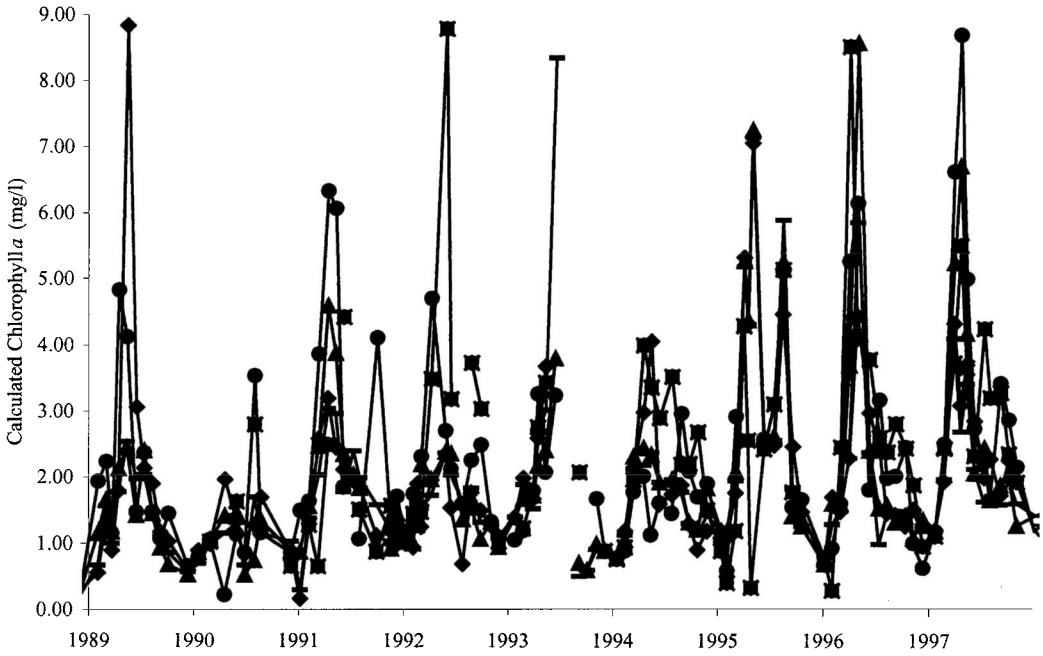


FIGURE 8. Calculated chlorophyll *a* concentrations at MI (◆), CNWS (–), CS (▲), SPB (●), and central San Francisco Bay (■).

from which high-salinity water can be tidally advected into San Pablo Bay, can peak in both spring and summer, but they show no hydrologically consistent pattern, because high values occur during dry and wet years. Thus, it is a combination of river-transported carbon, locally derived phytoplankton (which peaks in spring and fall in wet years, Figure 8), and marine phytoplankton (which peaks in spring and summer) that provides the near-continuous food source for this population (Figure 8). These multiple sources are apparently sufficient to support near-continuous reproduction (10 months of the year) during dry years (Figure 3).

Although there are large differences in the reproductive patterns of Suisun Bay and San Pablo Bay populations of *P. amurensis*, there is no evidence that the differences can be attributed to genetic differences. The bay population as a whole maintains high levels of genetic diversity, as measured in degrees of heterozygosity, levels of polymorphism, and the number of alleles per locus, but no distinct genetic difference was found between the populations sampled (Duda 1992). A high degree of genetic variability, allowing an organism to have flexibility to respond to changes in environmental factors, could be a factor in the variable reproductive strategies and, thus, the success of *P. amurensis* in colonizing and establishing itself in San Francisco Bay.

One of our motivating factors in doing this study was to examine the reproductive characteristics of *P. amurensis* that might contribute to its success as an invading species. In the estuarine environment, some of the factors that invading species must adapt to include seasonal variations in salinity, temperature, food supply, and predators. Presuming an invading species requires an opening in the community or a high number of propagules (Levine 2000), this opening can be used if individuals of a species have a greater tolerance to environmental extremes, the ability to outcompete an existing species in the utilization of a resource, and are capable of producing a large number of larvae under a wider variety of conditions. It has been shown that

P. amurensis larvae are capable of surviving a large range in salinity and temperature (Nicolini and Penry 2000). Thus, it is likely that once *P. amurensis* settled into San Francisco Bay, its ability to (1) utilize locally available, but varying sources of food resources to maximize reproductive activity, (2) withstand and reproduce during wide changes in salinity and temperature, and (3) survive as a larva in a wide range of salinities and temperatures allowed *P. amurensis* to produce many larvae and establish a continuing presence in the benthic community of San Francisco Bay.

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